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Reification, Matrices, and the Interrelationships of Goblin Spiders (Araneae, Oonopidae)

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In a recent review of the interrelationships of goblin spiders (the family Oonopidae), Platnick et al. (2012) presented a new subfamily-level classification of the family, replacing older arrangements that included at least one paraphyletic group. That analysis was based heavily on new evidence obtained, by an international consortium of researchers, through scanning electron microscopy of the tarsal organs, tiny chemoreceptors found near the tips of the legs and pedipalps.

The tarsal organ data supplied new information supporting the monophyly of the family, as well as characters relevant to understanding relationships among its genera (the family currently includes over 1000 species in over 85 genera; see Platnick, 2012). These data also supplied an example of a kind of character variation that creates problems with the conventional application of clustering algorithms to matrices. Most oonopids show a pattern of 3-3-2-2 raised receptors on legs I-IV, respectively. However, members of two genera seem to have a pattern of 4-4-3-3 receptors instead, and members of at least one other genus probably have a 2-2-1-1 pattern.

Obviously, there is some state of the tarsal organ that is plesiomorphic for the family, but outgroup comparison doesn't provide a simple answer to the question of which state that is. The members of the putative sister group of oonopids, the family Orsolobidae, as well as those of the other two families currently placed in the superfamily Dysderoidea (the Dysderidae and Segestriidae), have very differently constructed tarsal organs, with different kinds of receptors whose homologies with those of oonopids are unclear. Indeed, in the absence of detailed studies of their histology and innervation, we are unable to homologize individual receptors across all the oonopid genera, much less across all four families.

Nevertheless, Platnick et al. (2012) hypothesized that the 4-4-3-3 pattern is plesiomorphic for oonopids; it is found, for example, in the subfamily Orchestininae, which has long been considered among the most basal of oonopids. In our view, the 3-3-2-2 pattern represents a reduction from the plesiomorphic pattern (i.e., the loss of one receptor on each leg). Previous and current studies of the interrelationships among the genera of Orsolobidae indicate that a more pronounced reduction in receptor numbers has also occurred within that family (Forster and Platnick, 1985; Szűts, in prep.). Some reviewers of our original manuscript suggested that when summarizing our observations in the form of a matrix, the presence of a 4-4-3-3 pattern could be construed as a feature uniting just two genera, the nearly worldwide genus Orchestina and a New Zealand endemic, Kapitia. It is indeed true that those two genera show a form of tarsal organ not known in any other spiders. However, we chose instead to present our data as two characters, viewing all oonopids as sharing a "tarsal organ with raised receptors only, in serially dimorphic pattern (either 4-4-3-3 or a modified, reduced form of that pattern, i.e., 3-3-2-2 or 2-2-1-1)." We also included, as a second character, the reduction to the 3-3-2-2 pattern.

Our analysis was recently critiqued by Nixon and Carpenter (in press), in the context of responding to comments by Platnick (in press) on an earlier paper (Nixon and Carpenter, 2012) in which they presented an idiosyncratic concept of homology. That concept exemplifies a fallacy, reification, that philosophers frequently detect—the treatment of an abstraction, such as a hypothetical construct, as if it were a real entity or event. As it happens, spiders are united by at least two putative synapomorphies – features found in all spiders and in no other organisms: abdominal spinnerets, through which their silk in emitted, and male pedipalps that are modified for sperm transfer. According to Nixon and Carpenter (in press), declaring "that spinnerets are a synapomorphy of spiders ... is also declaring that giraffes and hippos lack spinnerets because their common ancestor also lacked them—not because an ancestor had spinnerets and they have been lost." Whether or not Nixon and Carpenter wish to admit it, they have no actual knowledge about what the common ancestor of giraffes and hippos was, or of whether it did or did not have spinnerets. They, like everyone else,

merely have inferences they make from their preferred cladogram. Their quoted statement is a clear example of reification.

Does their instance of this fallacy matter? They note, with regard to arachnids and plants, that "we may wish to score some of them as inapplicable, in which case we are not making a comparison." But under their stated concept of homology, and the ontology they adopt, we are not actually free to do so, as in their view "if we are doing one of the amply funded 'tree-of-life' analyses, and we wish to include presence of spinnerets as a character, then we must also score the other taxa in our analysis as lacking spinnerets, be they arachnids or plants."

The "must" in that quoted phrase is completely imaginary; we could more realistically view the presence of spinnerets as a transformation, or modification. Since spinnerets occur on the abdomen of spiders, they are presumably a transformation of some kind of abdomen that lacks spinnerets, and the presence or absence of the modification could be coded as 1 or 0 in whatever set of taxa one might suppose have the relevant kind of abdomen (I presume that giraffes, hippos, and plants do not!), and as inapplicable in all others (such as birds and bacteria). Similarly, another spider synapomorphy, male pedipalps modified for sperm transfer, is clearly inapplicable to all taxa that lack pedipalps. Indeed, one could attempt to regard all characters as modifications of other characters, which are therefore either present or absent, and which could therefore be construed as inapplicable to whatever taxa do not have at least the unmodified form of the character. None of these possibilities, however, justify reification of the results. If Nixon and Carpenter are correct, and one must actually know that the common ancestor of giraffes and hippos had no spinnerets before grouping together all the species that do have them, then there simply are no justified groups, as such knowledge is unachievable.

Nixon and Carpenter (in press) also presented a "Modified data matrix" for oonopids (their Table 2) that is equally imaginary. They miscode the relevant character (their no. 2, dealing with tarsal organ receptor morphology) in at least four taxa (they claim that the genera *Sulsula*, *Dalmasula*, *Xiombarg*, and *Unicorn* have a 2-2-1-1 pattern). Had they bothered to read the cited paper (Platnick *et al.*, 2012), rather than merely examine its matrix superficially, they would have discovered that the state of the tarsal organ receptors in those four taxa is actually unknown (because the capsulate structure of their tarsal organs prevents examination of the receptors by scanning electron microscopy). Indeed, the presence of a 2-2-1-1 pattern in any oonopid is speculative, although it may be the case in *Cortestina*, which has a partially capsulate tarsal organ in which at least some of the receptors can be detected.

The terminal clade of seven genera in their Fig. 2 could be supported as a monophyletic group only if the 2-2-1-1 pattern is actually a modification of a 3-3-2-2 pattern, or vice-versa, and we presented no such hypothesis, instead acknowledging the likelihood (Platnick *et al.*, 2012: 32) that the character state tree within oonopids consists of independent reductions from the plesiomorphic 4-4-3-3 pattern to a 3-3-2-2 pattern, and from 4-4-3-3 to 2-2-1-1, in two different lineages (within the subfamilies Oonopinae and Sulsulinae, respectively). Moreover, their terminal clade requires that the most obvious synapomorphy of the subfamily Oonopinae, a transformation of the sperm duct within the male pedipalps (their character 5) into a state that is strikingly different from that shared by all other known spiders, is a parallelism between *Kapitia* and the other oonopines. If we are correct in hypothesizing that the 4-4-3-3 pattern is plesiomorphic within the Oonopidae, then the placement of *Kapitia* outside the subfamily Oonopinae is simply not defensible, as no evidence disputes the palpal character that unites *Kapitia* with the bulk of the genera in the family. The only such "evidence" is the 4-4-3-3 tarsal organ pattern that occurs in *Kapitia* and the subfamily Orchestininae, which we contend is merely a plesiomorphic resemblance.

In other words, our coding correctly reflects our partial ordering of the character states. We hypothesized only that the 4-4-3-3 pattern is the plesiomorphic one within the family, not that 2-2-1-1 is necessarily a modification of 3-3-2-2 (or, for that matter, that 3-3-2-2 is necessarily a modification of 2-2-1-1). Obviously, since outgroup comparison fails in this case (as none of the outgroups have tarsal organs that would be coded as identical to those of oonopids), it would be wonderful if ontogenetic evidence could be brought to bear, but knowledge of juvenile oonopids is still quite minimal, and to date no ontogenetic differences in tarsal organ morphology have been detected between the juveniles and adults of any oonopid species.

The fact remains that examples of this type show why it is important to consider characters carefully, and not simply to assume that superficial codings like Nixon and Carpenter's misinterpretation of character 2 in their Matrix 2 are reasonable conjectures, or that the concomitantly mistaken results of those kinds of codings (such as the cladogram in their Fig. 2) are in any way worthy of having synapomorphies "read" from them. Thorough character analysis seems far more likely to lead to accurate results than does simply reifying the results of clustering algorithms on gigomatrices (garbage-in/garbage-out matrices) into statements about the characters of unobserved and unobservable ancestors!

Nixon and Carpenter's stated concept of homology requires that all shared plesiomorphic absences be treated as homologs, and seems to have been concocted only to support their view that plesiomorphic states should be hypothesized only for binary presence/absence characters, not in more complex situations, where they should instead be "read" from

the results. Both positions are thoroughly unconvincing exercises in reification. No one need claim that birds, mammals, strawberries, and bacteria all share a homology in lacking spinnerets or pedipalps, just to cluster all spiders together. No one need adopt a homology concept or ontology that requires such claims, much less construct gigomatrices that include them. No one need reify mere negative evidence (i.e., the lack of "observations" of inapplicable character states like the modified male pedipalps of stringbeans and corn) into (pseudo)homologies. Some beans should simply not be reified!

Under Nixon and Carpenter's homology concept, the acquisition of some detail of palpal morphology in a pair of sister species of oonopids somehow creates a homologous character state (the absence of that modification) that is shared by all the other 1.8 million described species on the planet. In reality, the synapomorphy uniting those two goblin spider species tells us nothing about the relationships of hippos and giraffes, other than that they are not members of the group that includes only the two oonopid species (i.e., it is simply inapplicable to such taxa). Reification of such 0 entries in some gigomatrix into anything other than mere negative evidence is unsupportable, undesirable, and unnecessary.

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